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Intestinal Helminth Parasites of Wall Lizards, *Podarcis vaucheri* Complex (Sauria: Lacertidae) from Algeria

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Abstract.—**A parasitological survey was carried out to determine the relationships between the helminth fauna and biological traits of the hosts in three Algerian populations of *Podarcis* lizards belonging to two different evolutionary lineages. Size, sex, and locality of collection, as well as the infracommunities and component communities, were analyzed. Very low values of parasite infection parameters and diversity were found in all three populations. This is in accordance with the feeding habits of these lizard hosts, which only eat animal prey and no plant matter. *Spauligodon saxicolae* (Nematoda: Pharyngodonidae), a specialist in lizards, is reported here for the first time in Africa. This nematode was the dominant parasite species for the three populations of lizards regardless their phylogenetic lineage, size, sex, and environmental conditions.**

Phylogenetic studies of the wall lizards genus *Podarcis* (Squamata: Lacertidae) from the Iberian Peninsula and North Africa have revealed cryptic speciation and considerable phylogeographic structure (Harris and Sá-Sousa, 2001, 2002; Harris et al., 2002; Pinho et al., 2006, 2007a,b, 2008) deriving from the complex paleogeological context in which they are found (Carretero, 2008). Distribution models (Sá-Sousa, 2000, 2001), morphometrics analyses (Sá-Sousa et al., 2002; Kaliontzopoulou et al., 2005) and behavioral experiments (Barbosa et al., 2005, 2006) carried out with the representatives of the Iberian Peninsula are mostly in agreement with the phylogenetic results. However, discrepancy between genetic markers (Pinho et al., 2007a, 2008) and instances of hybridization and introgression between lineages have also been recorded (Pinho et al., 2009; Renoult et al., 2009). To clarify relationships, more information on the ecological interactions of this complex lizard group is needed, including host–parasite relationships (Carretero, 2008; for a general review of this topic, see Bordes and Morand, 2009). Analyses of the gastrointestinal helminths of several western Iberian *Podarcis* indicate low infection rates and low species richness in accordance with a strictly entomophagous diet (Roca et al., 1989; Galdón et al., 2006; Roca et al., 2006).

However, much less, is known for the North African *Podarcis*, ascribed to the *Podarcis vaucheri* complex (Busack et al., 2005). There, wall lizards are not ubiquitous as in Europe but are restricted to cold, humid, and forested regions where their range has been fragmented between mountain massifs (Kaliontzopoulou et al., 2008). Until very recently, Algerian populations constituted the main knowledge gap for this complex. Fortunately, previous logistical problems have been overcome and Algerian wall lizards have finally been characterized phylogenetically. As many as four divergent lineages (Moroccan, Tunisian, Aurés and Azazga), whose taxonomic status remains doubtful, have been identified (Lima et al., 2009). Based on mitochondrial DNA calibrations, the divergence between such lineages has been hypothesized to be Pliocenic, associated with progressive climate aridification (Lima et al., 2009). Preliminary analyses also suggest phenotypic distinctiveness at least between two of them (Moroccan and Aurés lineages; Larbes et al., 2007), as well as a strictly carnivorous diet (Larbes, unpubl. data), but helminth communities remain unexplored.

Here, we aim to investigate the relationship between helminth and some host traits in two of the phylogenetic lineages of Algerian *Podarcis*, specifically addressing whether the structure of the helminth communities (1) changes to the host lineage and locality, (2) is related with the general patterns of the host diet, and (3) is affected by the size and sex of the host.

Materials and Methods

Sampling was conducted in three well-separated localities from Northern Algeria in spring 2006. These were, from east to west, the Belezma Natural Park (35°34′N 06°04′E, 1,250 m a.s.l.) in the Aurés, an isolated massif from northeastern Algeria; the Djurjura Massif (36°28′N 03°59′E, 1,520 m a.s.l.) in the Grand Kabylia, North–Central Algeria; and the Tiaret Plateau (35°17′N 01°15′E, 1,150 m a.s.l.) in northwestern Algeria. Under the influence of the Mediterranean Sea, Djurjura displays a cool subhumid climate and a vegetation dominated by forests (*Quercus canariensis*, *Quercus suber*, *Quercus ilex*, *Pinus halepensis*, and *Cedrus atlantica*). In contrast, Belezma and, mainly, Tiaret are continental sites with subhumid to dry semi-arid climate and more open vegetation structure (*Juniperus sp.* and other Mediterranean shrubs with scattered *Q. ilex*, *P. halepensis*, *C. atlantica*) (Le Houérou, 1989). According to the Worldclim database (http://www.worldclim.org/bioclim; Hijmans et al., 2005), annual mean temperature and precipitation are 12.5°C, 41 cm for Belezma; 15.7°C, 74 cm for Djurjura; and 14.9°C, 47 cm for Tiaret.

Lizard hosts inhabiting these sites belong to two different phylogenetic lineages within the *P. vaucheri* species complex (Lima et al., 2009): Lizards from Tiaret and Djurjura belong to the so-called Moroccan lineage, also occurring in northwestern Algeria; and those Belezma belonging to the Algerian endemic Aurés lineage. A total of 94 specimens were collected from three sites, all of them harboring dense lizard populations (Table 1). Lizards were sacrificed humanely by injection of sodium pentobarbital and used not only for this study but also for morphometrics (Larbes et al., 2007), diet (Larbes, unpubl. data), and phylogenetic analyses (Lima et al., 2009).

For each lizard, snout–vent length (SVL) was measured with calipers (±0.01 mm). Digestive tracts were removed, fixed in 70% ethanol, and were sent to the laboratory for parasitology analysis. For each lizard, the body cavity, digestive tract, heart, lungs, and liver were removed, opened, and placed in Ringer's solution for examination. Helminths were removed, washed, fixed, and mounted according to standard techniques (Roca, 1985). Parasites were identified, when possible, to species; and the number and location of individuals of each species were recorded.

The host vouchers were deposited in the herpetological collection of Centro de Investigação em Biodiversidade e Recursos Genéticos, University of Porto, Portugal, with the codes CIBIO-SL1 to CIBIO-SL11 and CIBIO-SL13 to CIBIO-SL93. The parasite vouchers were deposited in the parasitological collection of the Department of Zoology, University of Valencia, Spain, with the following codes: *Mesocestoides* sp. tetrathyridia: DZUV-MSPK; *Spauligodon saxicolae*: DZUV-SSB, DZUV-SSTK, DZUV-SST; *Skrjabinelazia* sp.: DZUV-SKSPK; *Acuaria* sp. (larvae): DZUV-ASPK; and Spirurida gen sp. (larvae): DZUV-SPIGENB, DZUV-SPIGENK; all of them were accompanied by the host code from CIBIO.

The use of descriptive ecological terms followed Bush et al. (1997). Brillouin's Index was used for calculating diversity according to Magurran (2004).

Results

Considering all localities together, five helminth species were recorded from the examined hosts (Table 1): one Cestoda (*Mesocestoides* sp. tetrathyridia) and four Nematoda (*S. saxicolae* Sharpilo, 1961, *Skrjabinelazia* sp., *Acuaria* sp., and Spirurida gen. sp.). *Mesocestoides* sp., *Acuaria* sp., and Spirurida gen sp. were recorded as larval forms and were located in the body cavity of their hosts. *Spauligodon saxicolae* and *Skrjabinelazia* sp. were adults, the first located at the end of the large intestine (rectum), and the second in the small intestine, respectively.

The global prevalence was 29%. Abundance and richness of helminth species in the communities of the host both locality and pooled were very low (Table 2). Significant differences in parasite abundance were detected between localities but not between host sexes (two-way ANOVA; locality: $F_{2,88} = 7.66$, $P < 0.001$; sex: $F_{1,88} = 0.99$, $P = 0.32$; locality × sex: $F_{2,88} = 0.84$, $P = 0.43$). This was likely a result of

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TABLE 1. Infection parameters of helminth species considering the host lineage, locality, and class. Values are given as the mean ± SE with the range in parentheses.

Helminth	Locality	Host lineage	Host class	*N*	Prevalence	Abundance
Cestoda						
Mesocestoides sp.	Belezma	Aurés	Pooled	38	–	–
	Djurjura	Moroccan	Pooled	51	2%	0.02 ± 0.02 (0–1)
	Tiaret	Moroccan	Pooled	5	–	–
	Pooled	Pooled	Pooled	94	1%	0.01 ± 0.01 (0–1)
Nematoda						
Spauligodon saxicolae	Belezma	Aurés	Pooled	38	24%	0.47 ± 0.18 (0–6)
	Belezma	Aurés	Males	19	21%	0.37 ± 0.17 (0–2)
	Belezma	Aurés	Females	19	26%	0.58 ± 0.33 (0–6)
	Djurjura	Moroccan	Pooled	51	16%	0.24 ± 0.09 (0–3)
	Djurjura	Moroccan	Males	30	17%	0.23 ± 0.11 (0–3)
	Djurjura	Moroccan	Females	21	14%	0.24 ± 0.15 (0–3)
	Tiaret	Moroccan	Pooled	5	60%	3.60 ± 2.46 (0–13)
	Pooled	Pooled	Pooled	140	21%	0.51 ± 0.17 (0–13)
Acuaria sp.	Belezma	Aurés	Pooled	38	–	–
	Djurjura	Moroccan	Pooled	51	2%	0.02 ± 0.02 (0–1)
	Tiaret	Moroccan	Pooled	5	–	–
	Pooled	Pooled	Pooled	94	1%	0.01 ± 0.01 (0–1)
Skrjabinelazia sp.	Belezma	Aurés	Pooled	38	–	–
	Djurjura	Moroccan	Pooled	51	2%	0.04 ± 0.04 (0–2)
	Tiaret	Moroccan	Pooled	5	–	–
	Pooled	Pooled	Pooled	94	1%	0.02 ± 0.02 (0–2)
Spirurida gen. sp	Belezma	Aurés	Pooled	38	5%	0.21 ± 0.19 (0–7)
	Djurjura	Moroccan	Pooled	51	4%	0.06 ± 0.04 (0–2)
	Tiaret	Moroccan	Pooled	5	–	–
	Pooled	Pooled	Pooled	94	4%	0.12 ± 0.08 (0–7)

the high infection rates of Tiaret lizards (Scheffé post hoc tests Belezma–Djurjura $P = 0.68$, Belezma–Tiaret $P < 0.001$, Djurjura–Tiaret $P = 10^{-3}$). No significant differences were found when this population was removed from the analysis (two-way ANOVA; locality: $F_{2,88} = 1.82$, $P = 0.17$; sex: $F_{1,88} = 2.66$, $P = 0.11$; locality × sex: $F_{2,88} = 1.09$, $P = 0.34$). Diversity was zero in all cases because no more than one parasite species was found simultaneously in a single host. Thus it was unnecessary to calculate asymptotic population diversities.

The only pharyngodonid nematode found was *S. saxicolae*, being the dominant helminth in all localities and the only one present in Tiaret. In fact, this species was responsible for the differences in parasite abundance (two-way ANOVA locality: $F_{2,88} = 10.52$, $P = < 0.001$; sex: $F_{1,88} = 1.95$, $P = 0.17$; locality × sex: $F_{2,88} = 0.87$, $P = 0.42$) because it was found more abundantly in Tiaret than in the other two localities (Scheffé post hoc tests: Belezma–Djurjura, $P = 0.74$; Belezma–Tiaret, $P = <0.001$; Djurjura–Tiaret, $P = <0.001$).

No differences in host size were detected between localities and sexes (two-way ANOVA locality: $F_{2,88} = 2.52$, $P = 0.08$; sex: $F_{1,88} = 0.03$, $P = 0.85$; locality × sex: $F_{2,88} = 1.26$, $P = 0.29$). However, when excluding the small sample size of Tiaret, sexual size dimorphism was evident suggesting larger males (two-way ANOVA locality: $F_{1,79} = 0.08$, $P = 0.78$; sex: $F_{1,79} = 5.56$, $P = 0.02$; locality × sex: $F_{1,79} = 1.54$, $P = 0.22$). Because of this and also because of some trend for increasing infection rate with host size (Fig. 1), analyses were repeated using the host size (SVL) as a covariate. Nevertheless, results remained the same. The differences between the sexes in parasite abundance and the high vales for Tiaret were confirmed by two-way ANCOVA (locality: $F_{2,87} = 20.83$, $P = 7 \times 10^{-4}$; sex: $F_{1,87} = 1.01$, $P = 0.32$; locality × sex: $F_{2,87} = 0.78$, $P = 0.46$) and Scheffé post hoc tests (Belezma–Djurjura, $P = 0.67$; Belezma–Tiaret, $P = 10^{-3}$; Djurjura–Tiaret, $P = 2 \times 10^{-4}$). We similarly found no differences in richness (two-way ANCOVA; locality: $F_{2,87} = 1.62$, $P = 0.20$; sex: $F_{1,87} = 2.75$, $P = 0.10$; locality × sex: $F_{2,87} = 0.91$, $P = 0.41$). Seemingly, this was a result of the differences in the abundance of *S. saxicolae* (two-way ANCOVA locality: $F_{2,87} = 21.82$, $P = 10^{-4}$; sex: $F_{1,87} = 1.92$, $P = 0.17$; locality × sex: $F_{2,87} = 0.86$, $P = 0.42$; Scheffé post hoc tests: Belezma–Djurjura, $P = 0.76$; Belezma–Tiaret, $P = 10^{-5}$; Djurjura–Tiaret, $P = 2 \times 10^{-5}$).

DISCUSSION

Our results confirm previous findings, suggesting that small carnivorous reptiles harbor poorer helminth communities than herbivorous ones (Petter and Quentin, 1976; Martin et al., 2005; Carretero et al., 2006).

Specifically regarding *Podarcis*, Algerian wall lizards harbored similar (or even poorer) helminth communities than *Podarcis bocagei* and *Podarcis carbonelli* from northwestern Iberian Peninsula which were also strictly carnivorous (Galdón et al., 2006; Roca et al., 2006). The helminth communities of these continental species contrast to the higher parasite richness and abundance found in the omnivorous *Podarcis pityusensis* and *Podarcis liffordi* inhabiting the Balearic Islands (Roca and Hornero, 1994). However, insularity per se is not the proximate factor promoting diversification in helminth communities. Microinsular populations of *Podarcis erhardii* in the Aegean, isolated during the Pleistocene and still strictly carnivorous (Adamopoulou et al., 1999), harbored depauperate parasite faunas when compared with their mainland relatives as a result of isolation and lack of intermediate hosts (Roca et al., 2009). Instead, herbivory may arise secondarily after long-term evolution in insularity (Van Damme, 1999; Carretero, 2004), and only then will helminth diversity in lizards increase. Because Algerian *Podarcis* consume only animal matter (Larbes, unpubl. data), they were expected to support poor and isolationist communities (see Aho, 1990; Martin and Roca, 2004). They can then be placed near the end of carnivory in the herbivory–carnivory continuum (Roca, 1999) and near the end of isolationism in a continuum of the isolationist

TABLE 2. Global infection and diversity parameters in the three host populations. Diversity, calculated using the Brillouin Index only with the parasitized hosts, was 0 in all cases. Values are given as the mean ± SE with the range in parentheses.

Locality	Host lineage	*N*	Prevalence	Abundance	Richness
Belezma	Aurés	38	29%	0.68 ± 0.25 (0–7)	0.29 ± 0.07 (0–1)
Djurjura	Moroccan	51	25%	0.35 ± 0.10 (0–3)	0.25 ± 0.06 (0–1)
Tiaret	Moroccan	5	60%	3.60 ± 2.46 (0–13)	0.60 ± 0.24 (0–1)
Pooled	Pooled	94	29%	0.67 ± 0.18 (0–13)	0.29 ± 0.05 (0–1)

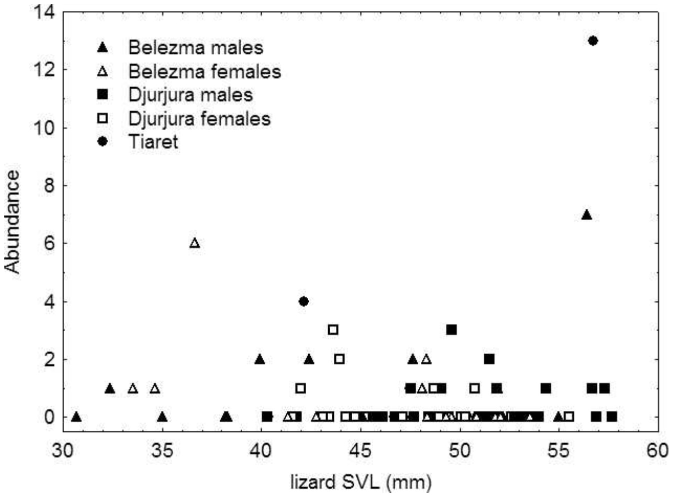

FIG. 1. Variation in the parasite abundance with size, locality, and sex of the host in three populations of Algerian *Podarcis.*

(poor)–interactive (rich) helminth communities (Roca et al., 2006). In this context, the low-parasite diversity found in all the intestine tracts must be considered more a by-product of low parasitization rather than arising from negative interactions between parasite species.

Spauligodon saxicolae is considered a lizard specialist (Edwards and Bush, 1989); the only lacertids described as parasitized by this species are the Caucasian *Darevskia* (*Darevskia saxicola* and probably other members of the genus; Sharpilo, 1961), and the Iberian lacertid *Podarcis hispanica* (Roca et al., 1986). Remarkably, *S. saxicolae* was the most frequent and abundant in all three localities and remained when the others disappeared, accounting for differences in the overall parasite abundance. Certainly, the differences between Tiaret and the other two localities may be attributed to low sample size. However, the abundance of *S. saxicolae* in the two localities with higher sample sizes (Belezma and Djurjura) can be considered representative, and attains values equivalent to those of the congeneric *Spauligodon carbonelli* parasitizing *P. bocagei* and *P. carbonelli* in Iberian Peninsula (Roca et al., 2006). In contrast to such cases, differences with sex and host size are minimal probably because only adult or subadult lizards were analyzed and their sexual size dimorphism was slight. In other lacertid lizards where prevalence increased with size, this seems to be just an indicator of lizard age, hence, of time for parasite recruitment (Roca et al., 1990; Sanchís et al., 2000; Martin et al., 2005; Carretero et al., 2006).

However, the presence of *Skrjabinelazia* sp. is not surprising, because many species of this genus are distributed around the world. Namely, several members of the genus have been recorded in Iberian Peninsula (Roca et al., 2006), Canary Islands (Martin and Roca, 2004), and Africa (Caballero, 1968). Nevertheless, this is the first record of a species of the genus from lizards from North Africa.

Furthermore, *Mesocestoides* sp., *Acuaria* sp., and Spirurida gen sp. were found as larval stages, as found in other *Podarcis* (Burke et al., 2007). This suggests that the Algerian *Podarcis* may be intermediate or paratenic hosts in the life cycle of these three species. The ultimate host is presumably a predator of the lizards (possibly a bird or a mammal).

Finally, in the framework of the evolutionary relationships within the *P. vaucheri* complex (Lima et al., 2009), these results do not provide evidence of distinction between the helminth communities of Moroccan and Aurés lineages. This may suggest secondary contacts between them allowing interchange of the parasites with direct cycle (*S. saxicolae*). However, morphological conservativeness of heminths suggests that caution should be used when making biogeographic inferences before a complete molecular analysis of the parasites can be carried out (Jorge, Roca, Perera, Harris, and Carretero, unpubl. data).

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